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MYCORRHIZAL COLONIZATION, HYPHAL LENGTHS, AND SOIL MOISTURE ASSOCIATED WITH TWO *ARTEMISIA TRIDENTATA* SUBSPECIES

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ABSTRACT.—Mycorrhizal fungi are thought to benefit associated plant species via enhanced nutrient uptake and/or improved water relations. However, detailed descriptions of the components of mycorrhizal colonization and mycor-rhizal hyphal growth are not available for *Artemisia tridentata*. This species occupies sites characterized by relatively low levels of both soil nutrients and moisture. We studied patterns of vesicular, arbuscular, and hyphal mycorrhizal colonization, mycorrhizal hyphal lengths, and soil moisture associated with two subspecies of *A. tridentata* over a 2-year period. *A. tridentata* ssp. *vaseyana* (ATV) is generally associated with more mesic and slightly higher elevation sites compared to *A. tridentata* ssp. *tridentata* (ATT). Nearly twice as much precipitation was received the first year compared to the second. In general, there were higher levels of colonization and hyphal lengths associated with ATV than with ATT. The ATV site received slightly more precipitation and was lower in available nutrients than the ATT site. Hyphal lengths and arbuscular colonization appeared more responsive to precipitation than were either vesicular or hyphal colonization. Hyphal colonization did not necessarily follow the same temporal pattern as hyphal lengths. Thus, mycor-rhizal activity was greater for the subspecies that received slightly more precipitation and occupied a site lower in available nutrients. Arbuscular colonization and hyphal lengths appeared to be most closely associated with soil moisture and thus plant activity.

Key words: *vesicular-arbuscular mycorrhizae, hyphal length*, Artemisia tridentata, *soil moisture, soil temperature.*

Understanding ecosystem processes requires baseline data that describe spatial and temporal variations in microbial mediated processes (Burke et al. 1989). Such information is also needed to assess the role of mycorrhizae and other fungi in native plant communities. In native plant communities, vesicular-arbuscular mycorrhizal (VAM) colonization has been shown to vary both seasonally and among plant species (Read et al. 1976, Rabatin 1979, Daft et al. 1980, Gay et al. 1982, Allen 1983, Giovannetti 1985, Brundrett and Kendrick 1988). Morphogenesis of arbuscule and vesicle formation should be differentiated when assessing functionality or dependency of the plant on VAM on a seasonal basis. The presence of arbuscules indicates plant-fungal interactions (Hirrel et al. 1978, Allen 1983) since arbuscules are the site for P and C transfer between symbionts (Cox and Tinker 1976, Wilcox 1993). Seasonal changes in extramatrical VAM fungal hyphae indicate that plant-fungal interactions are dynamic (Wilcox 1993). Therefore, it is necessary to measure seasonality

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of arbuscular colonization and extramatrical hyphae to adequately assess the changing relationship between symbionts in the field.

The Great Basin environment is characterized by winter precipitation, normally as snow, followed by hot, dry summers (Comstock and Ehleringer 1992). Root growth is most abundant in upper soil horizons in the early spring. Rooting activity diminishes in upper soil horizons as root growth follows the soil moisture profile into deeper soil layers (Fernandez and Caldwell 1975). In desert soils, N and P are most abundant in upper soil horizons (West 1991), and their availability to plants diminishes with decreasing soil moisture. Moisture movement from deep roots in moist soils to shallow roots in dry soils could make shallow soil nutrients available through the process of hydraulic lift (Passioura 1988, Caldwell and Richards 1989, Caldwell et al. 1991). Mycorrhizae could play a role in this process (Richards and Caldwell 1987, Caldwell et al. 1991); however, little is known about seasonal dynamics of mycorrhizae in arid ecosystems.

Fitter (1993) suggests that plant root systems evolve in a manner that optimizes the use of plant carbon. Mycorrhizal colonization and the formation of extramatrical hyphae should also reflect an optimization of plant carbon usage. But to date there is relatively little information on spatial or temporal variation in mycorrhizal activity in the Great Basin. In this study we quantified VAM arbuscular root colonization, vesicular root colonization, hyphal root colonization, and mycorrhizal hyphal length through the plant growing season for 2 years in *Artemisia tridentata* ssp. *tridentata* and *Artemisia tridentata* ssp. *vaseyana*. We have characterized the seasonality of the above parameters and show their relationship to changes in both soil moisture and temperature.

STUDY SITE DESCRIPTION

An *Artemisia tridentata* ssp. *tridentata* (ATT) and an *Artemisia tridentata* ssp. *vaseyana* (ATV) plant community were chosen for study. The study sites are located approximately 30 miles northwest of Reno, Nevada, and are within 3 miles of each other. The ATT community is at 1555 m elevation and is composed of the following vegetation: *Artemisia tridentata* ssp. *tridentata, Chrysothamnus viscidiflorus, Ephedra viridis, Stipa comata, S. thurberiana,*

Oryzopsis hymenoides, Elymus hystrix, and *Bromus tectorum.* The soil is classified as a coarse-loamy, mixed, mesic Aridic Argixeroll. This is an alluvial fan soil that was mainly derived from granitic rocks. The soil consists of about 40 cm of loamy sand to gravelly loamy sand overlying a subsoil of about 50 cm of sandy loam. The underlying material to over 200 cm is loamy coarse sand.

The ATV community is at 1830 m elevation and includes the following vegetation: *Artemisia tridentata* ssp. *vaseyana, Purshia tridentata, Ribes* sp., *Chrysothamnus viscidiflorus, Stipa columbiana, S. occidentalis, Elymus hystrix,* and *Bromus tectorum.* The soil is classified as a coarse-loamy, mixed, frigid Ultic Argixeroll. This type of upland soil formed in a residuum from granodiorite and consists of about 60 cm of gravelly coarse sand and loamy coarse sand overlying a subsoil of about 30 cm of loamy coarse sand and sandy loam. The underlying material consists of about 10 cm of weathered granodiorite.

METHODS

Sampling was conducted on seven dates in 1989 and five dates in 1990. Four replicate macroplots (20×20 m) were randomly selected at each site. One shrub within a macroplot was selected for sampling each year. We changed shrubs to ensure that the prior year's sampling did not influence measured parameters. Within each macroplot a CR10 micrologger (Campbell Scientific, Logan, Utah)[3] was equipped to measure soil temperature at 10 cm and soil moisture at 10, 30, and 60 cm, adjacent to the target shrub. Soil temperatures were measured with thermocouples, and soil moisture with gypsum blocks. Leader length was measured as a plant growth indicator (Barker and McKell 1986) to avoid destructive harvest of *Artemisia* shrubs. Five marked leaders were measured on the target shrub within each macroplot at each sampling date.

Soil samples were collected with a spade to a depth of 20 cm from within the dripline of the target shrub in each macroplot on each date. Sample volumes were about 8000 cm³ ($20 \times 20 \times 20$-cm cube). Roots were sieved from soil, and both root and soil samples were placed in plastic bags and kept on ice prior to

storage at –2°C. During the sieving process we discarded non-*Artemisia* roots, which are easily differentiated by color and morphology. In the laboratory roots were washed and cut into 1-cm segments; they were then cleared with KOH and stained with trypan blue (Phillips and Hayman 1970). We estimated percent total, arbuscular, hyphal, and vesicular colonization using the gridline-intersect method with a compound microscope at 160X.

Hyphal lengths were quantified using the following modified Bethlenfalvay and Ames (1987) procedure: (1) 20 g of soil was added to 100 ml of 0.05% trypan blue solution and boiled for 15 min; (2) samples were cooled and 100 ml of sodium hexametaphosphate was added to each flask; (3) flask contents were added to a Waring blender and blended for about 5 sec; and (4) an aliquot was added to a microscope slide and scored for hyphal lengths at 400X. Hyphal lengths were measured on six different aliquots per soil slurry using an improved Neubauer ultra plane counting chamber with a depth of 0.1 mm. Four randomly selected transects from each aliquot were scanned at 400X. Each scan was 7.9 mm long and 0.395 mm wide. From these dimensions the liquid volume scanned was calculated (3.12×10^{-4} ml/ scan). Slides were scanned and hyphal lengths quantified using an image analysis system. Aliquots were averaged prior to statistical analysis. We tried a 1:50 soil to extractant ratio initially, but found we had to use 1:10 because VAM hyphal lengths were low. The 1:10 extraction has been shown by Ingham and Klein (1984) to be adequate for measuring hyphal lengths. Since roots were removed before extraction, VAM hyphal lengths presented do not include rhizoplane hyphae. Inclusion of rhizoplane hyphae would no doubt elevate hyphal lengths; however, exclusion of roots allows a more accurate depiction of the hyphae that extend beyond the zone of phosphorus depletion around roots. Criteria for determining VAM fungi were similar to those established by Allen and Allen (1986). Most mycorrhizal hyphae are branched, have a knobby appearance, are aseptate, absorb trypan blue, and are about 3–10 μm in diameter.

Soil samples collected from each site were composited each year for soil chemical and physical analyses. Nitrate, NH_4^+, and SO_4^{-2} were extracted using 0.1 M KCl; phosphorus was extracted using sodium bicarbonate (Olsen and Sommers 1982); organic carbon was determined using the Walkley-Black procedure (Nelson and Sommers 1982); and particle-size analysis was determined using standard methods (Gee and Bauder 1982).

Data were analyzed by year. *Artemisia* sites and sampling date effects were assessed using analysis of variance with SAS (Statistical Analysis System). All VAM root colonization data were transformed by taking the arcsine and square root of VAM root intersects per total root intersects prior to conducting analysis of variance.

RESULTS

The ATT site had significantly higher levels of bicarbonate extractable P, KCl extractable SO_4^{-2}, and KCl extractable NO_3^- than the ATV site (Table 1). ATT soils had a significantly lower proportion of sand and significantly more silt and clay than ATV soils. Organic carbon and NH_4^+ were not significantly different between the two sites. Neither soil chemical nor physical characteristics were significantly different between years (Table 1). The significant Site*Date interaction for extractable P is evident since P increases in the second year at the ATT site, yet decreases at the ATV site.

Leader lengths were shorter in both plant communities in 1990 than in 1989 (Fig. 1). In addition, leader length was slightly higher in the ATV community in both years. Decreased leader lengths in 1990 are attributed to lower

TABLE 1. Means and probability values for soil physical and chemical characteristics of the *A. tridentata* ssp. *tridentata* (ATT) and *A. tridentata* ssp. *vaseyana* (ATV) sites in 1989 and 1990. Soil samples used for mycorrhizal characterization were used in this analysis, which accounts for the change in textural analysis between years. Inorganic P (bicarbonate extractable), N (KCl extractable), S (KCl extractable), and Walkley-Black soil organic carbon (O.C.) are given in the table (n = 4[a]).

| Soil variable | ATT | | ATV | | |
	1989	1990	1989	1990	Site
% sand	84.2	80.4	91.1	92.3	.006
% silt	11.5	14.8	6.2	5.8	.008
% clay	4.3	4.9	2.8	1.8	.046
P μg g^{-1}	12.1	14.3	9.8	7.9	.0005
NH_4 μg g^{-1}	5.2	5.1	5.6	3.4	.39
NO_3 μg g^{-1}	6.6	8.3	4.6	4.0	.03
SO_4 μg g^{-1}	7.8	9.6	4.6	5.2	.001
O.C. mg g^{-1}	9.6	8.8	9.3	10.0	.62

[a]The effect of year was not significant (P > .05) for any variable, and only in the case of P was the Site and Year interaction significant (P < .05).
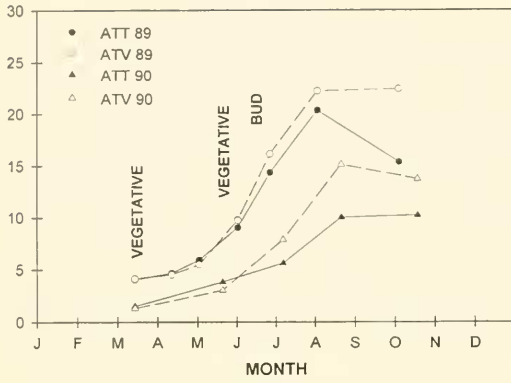
Fig. 1. Seasonal change in leader length for *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) during the 1989 and 1990 growing seasons. Phenological stage appears at the top of the graph.

precipitation received during that year (Fig. 2). Annual precipitation for the growing season was measured beginning in November. In 1989 ATT and ATV communities received 384 and 436 mm of precipitation, respectively. However, during 1990 the ATT and ATV communities received only 194 and 206 mm, respectively. The 4-year average precipitation (1984–87) for ATT and ATV was 211 and 256 mm, respectively.

The two sites were not different from each other in either maximum or minimum temperature (Fig. 2). Maximum March temperatures at 10-cm soil depths for both sites and years were 7–13°C, while minimum temperatures were 2–4°C. Maximum soil temperatures in July–August at 10 cm for both sites and years were 30–31°C, while corresponding minimum
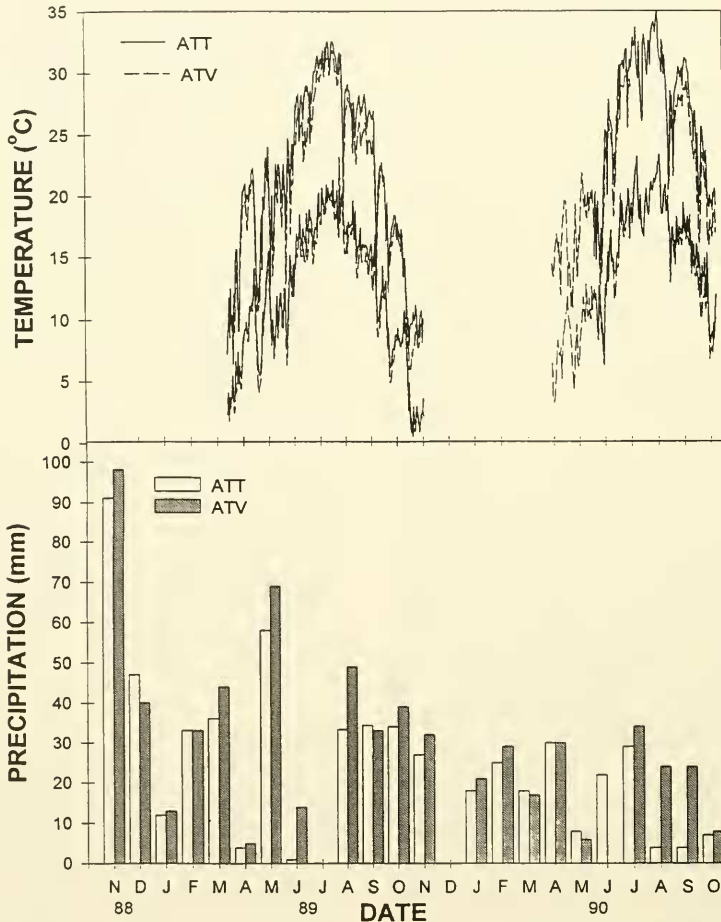

Fig. 2. Daily maximum and minimum soil temperatures at the 10-cm soil depth and monthly precipitation for *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) during the 1989 and 1990 growing seasons.

temperatures were 19–21°C. By mid-October maximum temperatures were 16–19°C and minimum temperatures were 8–9°C.

During early 1989 percent arbuscular colonization was similar for the two *Artemisia* subspecies but diverged to greater levels in ATV roots by early June (Fig. 3). Arbuscular colonization of ATT roots dropped to much lower levels than ATV roots during the midsummer dry period. This was followed by a minimal increase in colonization during fall for both subspecies. In 1990 percent arbuscular colonization was consistently lower for ATT than ATV roots (Fig. 4, Table 2). There was also a decrease in colonization from early spring through summer for both subspecies. Overall analysis of variance indicates a significant season and subspecies effect for percent arbuscular colonization in both years (Table 2).

In 1989 percent hyphal, vesicular, and total colonization did not significantly change through the season (Fig. 3, statistics in Table 2).

However, in 1990 both percent hyphal and total colonization changed significantly through the season (Fig. 4, statistics in Table 2). In both years a significant subspecies effect was observed for vesicular and total colonization. Subspecies *vaseyana* roots had greater levels of colonization than *tridentata* roots.

Mycorrhizal hyphal lengths changed significantly through the season for both years (Fig. 5, statistics in Table 2). In 1989 and 1990 hyphal length more than doubled from March to May for all sites except the ATV site in 1990. Hyphal lengths decreased during summer and remained constant during fall for all sites with the exception of ATV in 1990, which increased slightly during the fall. Mycorrhizal hyphal-lengths were significantly greater at the ATV site when compared to the ATT site for most sampling dates.

Soil moisture depletion data are presented in Figure 6. In both years the ATV site had higher soil water potentials for a greater proportion
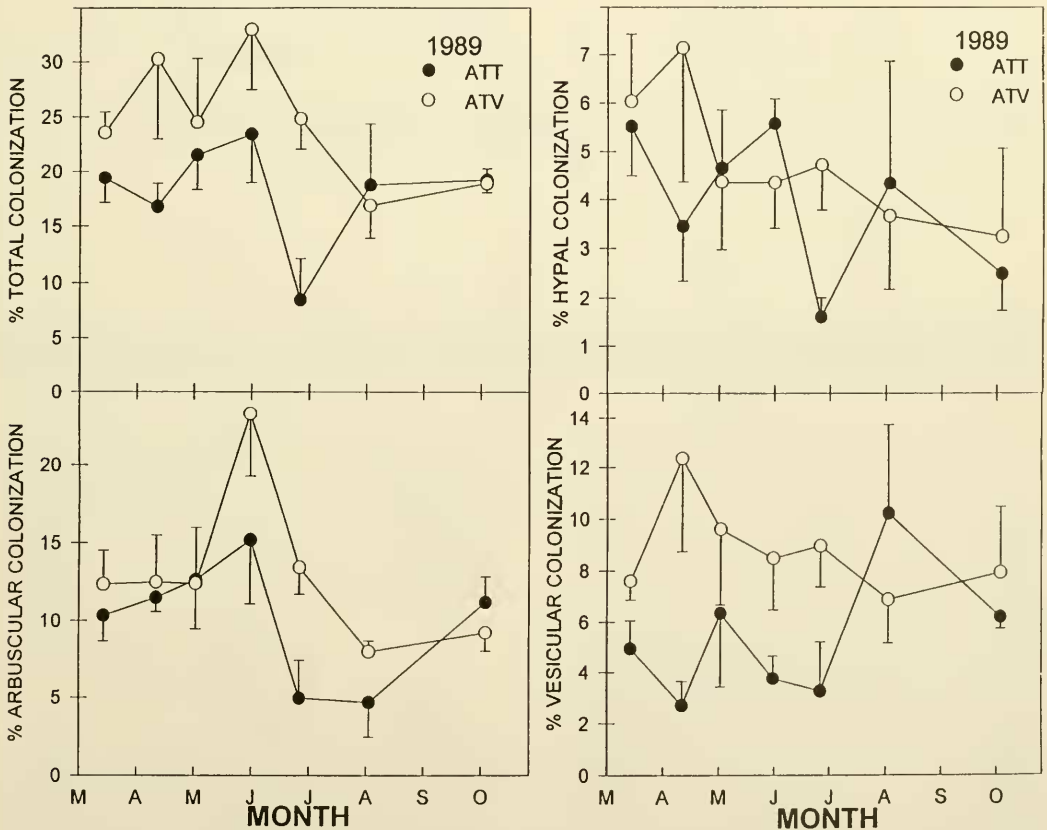

Fig. 3. Monthly changes in percent total, arbuscular, vesicular, and hyphal root colonization for *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) during the 1989 growing season.
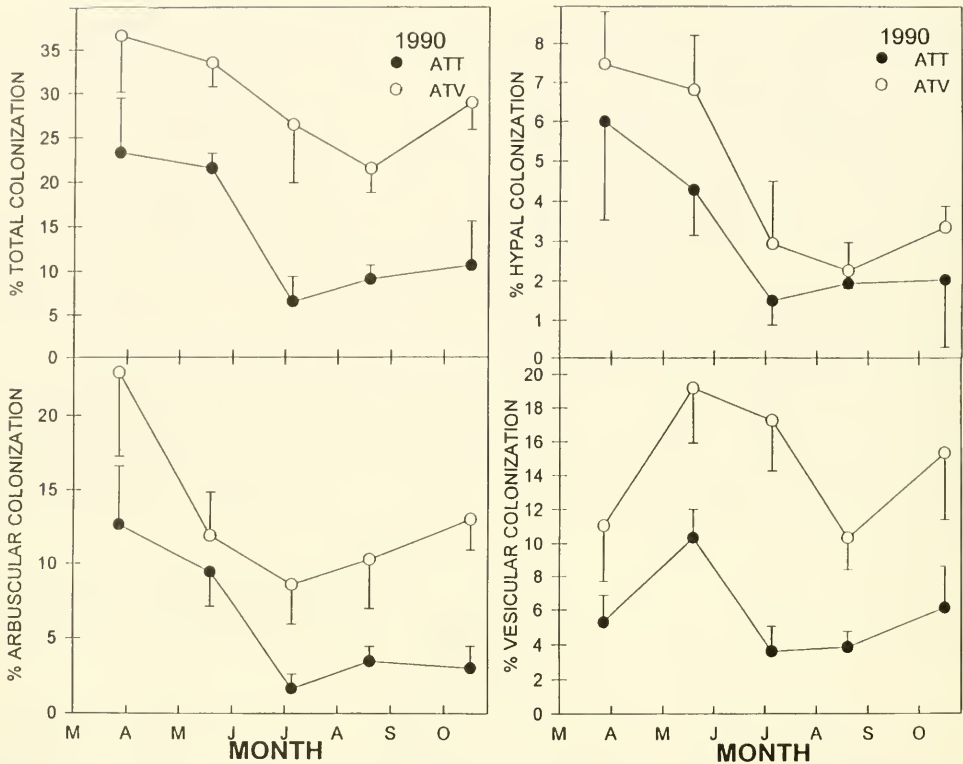
Fig. 4. Monthly changes in percent total, arbuscular, vesicular, and hyphal root colonization for *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) during the 1990 growing season.

TABLE 2. Site means and results of two-way ANOVAs showing the effect of sagebrush site (*Artemisia tridentata* ssp. *tridentata* vs. ssp. *vaseyana*) and time of year (Date) on mycorrhizal colonization (ARB = arbuscular colonization, VES = vesicular colonization, HYP = hyphal colonization, TOT = total colonization) and mycorrhizal hyphal length (mg^{-1}).

| | Site means[a] | | Probability values | | |
	ATT	ATV	Site	Date	Site*Date
			1989		
% ARB	10.1	13.1	.009	.014	.316
% VES	5.4	8.8	.004	.517	.031
% HYP	3.9	4.8	.346	.205	.563
% TOT	19.4	26.7	.004	.067	.149
Length	1.3	1.8	.018	.0004	.491
			1990		
% ARB	6.1	13.4	.0001	.005	.461
% VES	5.9	14.6	.0003	.116	.206
% HYP	3.1	4.6	.065	.003	.852
% TOT	15.1	32.6	.0001	.004	.511
Length	0.9	1.7	.005	.050	.373

[a]Site means were averaged over sampling date for each year (ATT = *Artemisia tridentata* ssp. *tridentata*, ATV = *Artemisia tridentata* ssp. *vaseyana*).
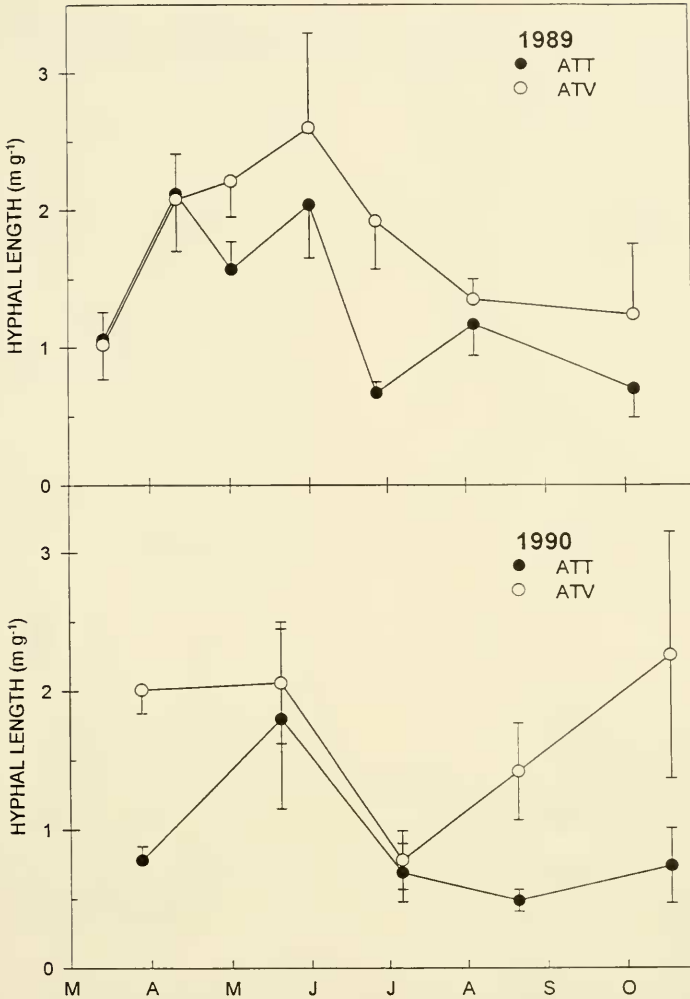
Fig. 5. Seasonal changes in mycorrhizal hyphal lengths (m of hyphae/g of soil) in soil adjacent to *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) during the 1989 and 1990 growing seasons.

of the season than did the ATT site. Soil moisture declined more rapidly in 1990 compared to 1989. Soil moisture at 10 and 30 cm fell below –1.5 MPa at both sites by midsummer 1990. In 1989 late summer and early fall precipitation raised soil water potentials above –0.2 MPa at both sites by October.

DISCUSSION

The two *Artemisia* subspecies exhibited consistent differences in both colonization and hyphal density of the associated mycorrhizae. Because the study was observational in nature, we could not separate genetics of two subspecies from the differences in sites they occu-

pied. Thus, differences must be attributed to the species/site combination. The ATV site was slightly more mesic than the ATT site, but we did not detect any differences in temperature (Fig. 2). In general, ATV tends to occupy sites of higher elevation or with more summer precipitation than ATT (e.g., Winward 1980). In this study we also found that on a seasonal average the ATV site was lower in available nutrients than the ATT site (Table 1). Nutrient differences may be the result of either plant community differences or the fact that the ATV site had a higher sand content. Higher levels of colonization and greater hyphal lengths at the ATV site compared to the ATT site were thus associated with more available
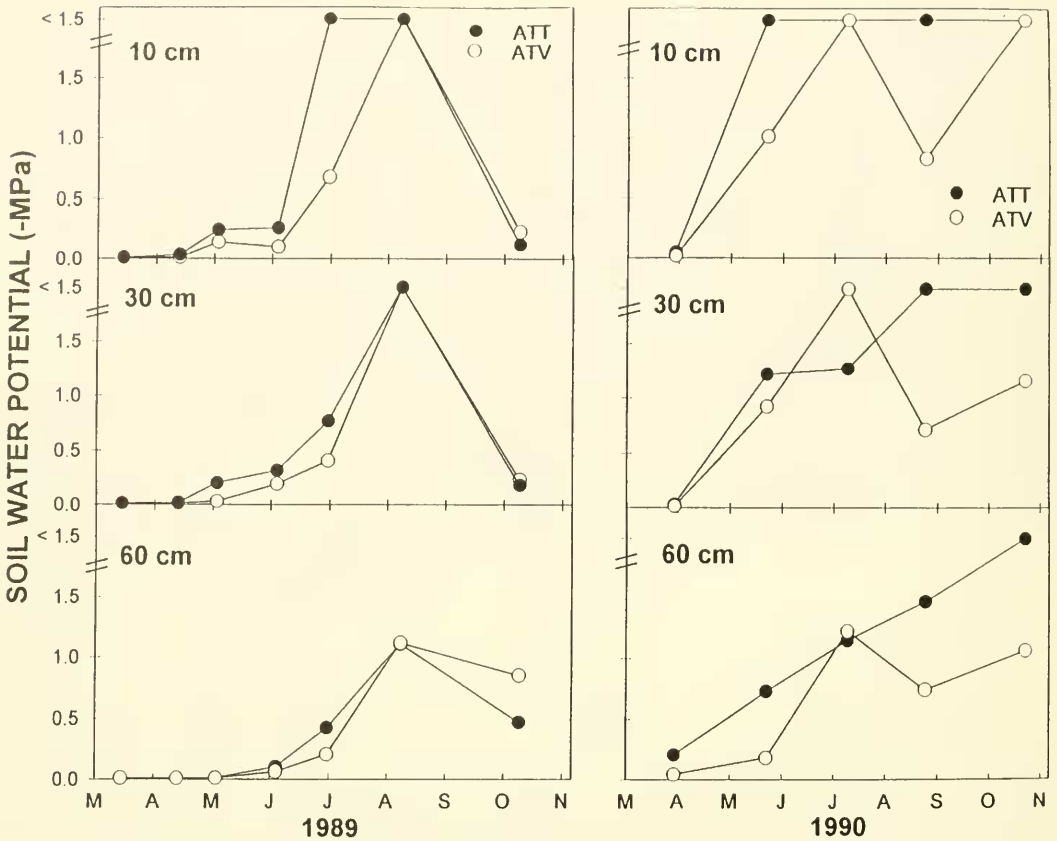
Fig. 6. Monthly change in soil water potential (–MPa) in *Artemisia tridentata* ssp. *tridentata* (ATT) and *Artemisia tridentata* ssp. *vaseyana* (ATV) plant communities. Water potentials were measured in 1989 and 1990 at 10-, 30- and 60-cm soil depths with gypsum blocks.

soil moisture and lower nutrient availability. These data tend to support the hypothesis that mycorrhizae are more active when moisture is available and nutrients are limiting.

Arbuscular colonization is thought to be particularly important to carbon and phosphorus exchange (Cox and Tinker 1976, Wilcox 1993), and thus this feature plays a critical role in plant/fungus interaction (Hirrel et al. 1978, Chilvers and Daft 1982, Allen 1983). The two study sites differed in arbuscular colonization during both years. However, the difference was more consistent during 1990 compared to 1989. The difference in P availability between sites was 23% in 1989 and 81% in 1990. Thus, the greatest separation in mycorrhizal activity between sites corresponded to the greatest differences in P availability.

Timing of maximal mycorrhizal activity appeared to correspond to aboveground activity during the higher precipitation year of

1989. Previous research has demonstrated that *A. tridentata* achieves highest photosynthetic rates during late spring when moisture is available and temperatures are generally not limiting (DePuit and Caldwell 1973). The peak in root growth of *A. tridentata* also occurs in mid-April to late May (Fernandez and Caldwell 1975). Our measurements of leader growth (Fig. 1) appear to confirm that peak aboveground activity occurred in late spring or early summer during this study. However, during the dry year of 1990 there was no increase in mycorrhizal activity during the spring; rather, activity generally declined. The fact that precipitation and leader growth in 1990 were roughly half of 1989 values indicates that environmental stress may have limited plant activity in 1990. Plant stress and limited carbon assimilation likely reduced root and/or mycorrhizal activity. Because mycorrhizal activity can be a rather substantial carbon cost to the

associated plant (Chapin et al. 1987), it is not surprising that mycorrhizal colonization and hyphal length would decline during a drought year.

Hyphal lengths appeared to be quite responsive to precipitation patterns within a year. Increases in hyphal lengths in the spring of 1989 were associated with spring precipitation. Hyphal lengths declined during the dry summer period and were stable during fall as both sites began receiving precipitation again. During 1990 hyphal lengths were stable during spring and declined during summer. In late summer and fall of 1990, the ATV site received precipitation and hyphal lengths increased (Figs. 5, 6). However, the ATT site did not receive significant precipitation and hyphal lengths did not increase. It appears that the pattern of arbuscular colonization more closely follows precipitation and hyphal lengths than does either vesicular or hyphal colonization. Arbuscular colonization and mycorrhizal hyphal lengths are more responsive to seasonal and yearly variations in plant growth than are either vesicular or hyphal colonization levels. We suggest, from a functional standpoint, that measurement of mycorrhizal hyphal length and arbuscular colonization is more relevant than is total colonization.

ACKNOWLEDGMENTS

LITERATURE CITED

ALLEN, M. F. 1983. Formation of vesicular-arbuscular mycorrhizae in *Atriplex gardneri* (Chenopodiaceae): seasonal response in a cold desert. Mycologia 75: 773–776.

ALLEN, E. B., AND M. F. ALLEN. 1986. Water relations of xeric grasses in the field: interactions of mycorrhizas and competition. New Phytologist 104: 559–571.

BARKER, J. R., AND C. M. McKELL. 1986. Differences in big sagebrush (*Artemisia tridentata*) plant stature along soil-water gradients: genetic components. Journal of Range Management 39: 147–151.

BETHLENFALVAY, G. J., AND R. N. AMES. 1987. Comparison of two methods for quantifying extraradical mycelium of vesicular-arbuscular mycorrhizal fungi. Soil Science Society of America Journal 51: 834–837.

BRUNDRETT, M. C., AND B. KENDRICK. 1988. The mycorrhizal status, root anatomy, and phenology of plants in a sugar maple forest. Canadian Journal of Botany 66: 1153–1173.

BURKE, I. C., W. A. REINERS, AND D. S. SCHIMEL. 1989. Organic matter turnover in a sagebrush steppe landscape. Biogeochemistry 7: 11–31.

CALDWELL, M. M., AND J. H. RICHARDS. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. Oecologia 79: 1–5.

CALDWELL, M. M., J. H. RICHARDS, AND W. BEYSCHLAG. 1991. Hydraulic lift: ecological implications of water efflux from roots. Pages 423–436 in D. Atkinson, ed., Plant root growth: an ecological perspective. Blackwell Scientific Publications.

CHAPIN, F. S., III, A. J. BLOOM, C. B. FIELD, AND R. H. WARING. 1987. Plant responses to multiple environmental stresses. Bioscience 37: 49–57.

CHILVERS, M. T., AND J. F. DAFT. 1982. Effect of low temperatures on development of the vesicular-arbuscular mycorrhizal association between *Glomus caledonium* and *Allium cepa*. Transactions of the British Mycological Society 79: 153–157.

COMSTOCK, J. P., AND J. R. EHLERINGER. 1992. Plant adaptation in the Great Basin and Colorado Plateau. Great Basin Naturalist 52: 195–215.

COX, G., AND P. B. TINKER. 1976. Translocation and transfer of nutrients in vesicular-arbuscular mycorrhizas. I. The arbuscule and phosphorus transfer: a quantitative ultrastructural study. New Phytologist 77: 371–378.

DAFT, M. J., M. T. CHILVERS, AND T. H. NICOLSON. 1980. Mycorrhizas of the liliiflorae. I. Morphogenesis of *Endymion nonscriptus* (L.) Garcke and its mycorrhizas in nature. New Phytologist 85: 181–189.

DePUIT, E. J., AND M. M. CALDWELL. 1973. Seasonal pattern of net photosynthesis of *Artemisia tridentata*. American Journal of Botany 60: 426–435.

FERNANDEZ, O. A., AND M. M. CALDWELL. 1975. Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. Journal of Ecology 63: 703–714.

FITTER, A. H. 1993. Characteristics and functions of root systems. Pages 3–24 in Y. Waisel, A. Eshel, and U. Kafkafi, eds., Plant roots: the hidden half. Marcel Dekker, Inc., New York, Basel, Hong Kong.

GAY, P. E., P. J. GRUBB, AND H. J. HUDSON. 1982. Seasonal changes in the concentrations of nitrogen, phosphorus and potassium, and in the density of mycorrhiza, in biennial and matrix-forming perennial species of closed chalkland turf. Journal of Ecology 70: 571–593.

GEE, G. W., AND J. W. BAUDER. 1982. Particle size analysis. Pages 383–409 in A. Klute, ed., Methods of soil analysis. Part 1. Physical and mineralogical methods. 2nd edition. Agronomy No. 9, Part 2. American Soil Association and Soil Science Society of America publication. Madison, Wisconsin.

GIOVANNETTI, M. 1985. Seasonal variations of vesicular-arbuscular mycorrhizas and endogonaceous spores in a maritime sand dune. Transactions of the British Mycological Society 84: 679–684.

HIRREL, M. C., H. MEHRAVARAN, AND J. W. GERDEMANN. 1978. Vesicular-arbuscular mycorrhizae in the Chenopodiaceae and Cruciferae: Do they occur? Canadian Journal of Botany 56: 2813–2817.

INGHAM, E. R., AND D. A. KLEIN. 1984. Soil fungi: relationships between hyphal activity and staining with fluorescein diacetate. Soil Biology Biochemistry 16: 273–278.

NELSON, D. W., AND L. E. SOMMERS. 1982. Total carbon, organic carbon, and organic matter. Pages 539–577 in A. L. Page, R. H. Miller, and D. R. Keeney, eds., Methods of soil analysis. Part 2. Chemical and microbiological properties. 2nd edition. Agronomy No. 9, Part 2. American Soil Association and Soil Science Society of America publication. Madison, Wisconsin.

OLSEN, S. R., AND L. E. SOMMERS. 1982. Phosphorus. Pages 403–427 in A. L. Page, R. H. Miller, and D. R. Keeney, eds., Methods of soil analysis. Part 2. Chemical and microbiological properties. 2nd edition. Agronomy No. 9, Part 2. American Soil Association and Soil Science Society of America publication. Madison, Wisconsin.

PASSIOURA, J. B. 1988. Water transport in and to roots. Annual review. Plant Physiologist 39: 245–265.

PHILLIPS, J. M., AND D. S. HAYMAN. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Transactions of the British Mycological Society 55: 158–161

RABATIN, S. C. 1979. Seasonal and edaphic variation in vesicular-arbuscular mycorrhizal infection of grasses by *Glomus tenuis*. New Phytologist 83: 95–102.

READ, D. J., H. K. KOUCHEKI, AND J. HODGSON. 1976. Vesicular-arbuscular mycorrhiza in natural vegetation systems. I. The occurrence of infection. New Phytologist 77: 641–653.

RICHARDS, J. H., AND M. M. CALDWELL. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73: 486-489.

WEST, N. E. 1991. Nutrient cycling in soils of semiarid and arid regions. Pages 295–332 in J. Skujins, ed., Semiarid lands and deserts: soil resource and reclamation. Marcel Dekker Inc., New York.

WILCOX, H. E. 1993. Mycorrhizae. Pages 731–767 in Y. Waisel, A. Eshel, and U. Kafkafi, eds., Plant roots: the hidden half. Marcel Dekker, Inc., New York, Basel, Hong Kong.

WINWARD, A. H. 1980. Taxonomy and ecology of sagebrush in Oregon. Oregon State University Station Bulletin 642.